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Evolutionary history of the Cenozoic bivalve genus *Kaneharaia* (Veneridae)

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Abstract. The evolutionary history of the bivalve genus *Kaneharaia* (Dosiniinae) is discussed. The genus *Kaneharaia* is restricted to the North Pacific region and contains four species : *K. kaneharai* (Yokoyama), *K. kannoi* (Masuda), *K. ausiensis* (Ilyina) and *K.* sp. *K. ausiensis* survived until the mid-Pliocene while the other three species became extinct at the end of the Miocene. In addition to these species, *Dosinia mathewsonii* from the upper Oligocene San Ramon Formation of California and *D. whytneyi* from the early middle Miocene Astoria Formation of Oregon most probably belong to the genus *Kaneharaia*. *Kaneharaia* evolved from the common ancestor with *Dosinia* because both genera share many common characteristics such as the subumbonal pit, the brown-coloured surface, and the finely crossed lamellar structure in the outer layer. Based on the fossil record, *Kaneharaia* first appeared in the northeastern Pacific during the late Oligocene and migrated westward during the early middle Miocene Climatic Optimum in the North Pacific.

Key words : Bivalvia, evolution, *Kaneharaia*, *Dosinia*, Dosiniinae

Introduction

Kaneharaia is an extinct genus of Dosiniinae (Bivalvia : Veneridae) which was first proposed as a subgenus of *Dosinia* Scopoli, 1777 by Makiyama (1936), based on *Dosinia kaneharai* Yokoyama, 1926 from the Miocene Kanomatazawa Formation in Tochigi Prefecture as its type species. Species of *Kaneharaia* have been found in the Miocene deposits of Honshu and Hokkaido, Japan, Sakhalin and Kamchatka, Russia and northern Korea, and also in the lower Pliocene of Honshu (Masuda, 1967 ; Amano, 1983 ; Gladenkov *et al*., 1987 ; Amano and Sato, 1995). Other than *K. kaneharai*, the following species and subspecies of *Kaneharaia* have been described : *K. kaneharai* (Yokoyama, 1926), *K. ausiensis* (Ilyina, 1954), *K. kaneharai ouchiensis* (Kanno, 1955), *K. kannoi* (Masuda, 1963), *K. kaneharai fujinensis* (Masuda, 1967), *K. kaneharai rumoiensis* (Amano,1983), *K. kaneharai uandiensis* (Sinelnikova, 1987 *in* Gladenkov *et al*., 1987).

Makiyama (1936) and Masuda (1967) pointed out that *Kaneharaia* is similar to *Dosinidia* Dall, 1902 (=*Dosinia* Scopoli, 1777) in the absence of escutcheon and lamellated concentric sculpture which are common characters in other Japanese dosiniine genera such as Phacosoma Jukes-Brown, 1912, *Dosinella* Dall, 1902 and Dosinorbis Dall, 1902. However, no detailed comparison of hinge structure between *Kaneharaia* and *Dosinia* has been made.

When they examined the shell microstructure of *Kaneharaia kaneharai* and *Phacosoma* spp., Kobayashi *et al*. (1968) and Hikida (1996) showed that the shell microstructure is a useful character for diagnosing some genera within Dosiniinae and separated *Kaneharaia* from *Phacosoma* as a distinct genus based on the difference of microstructure of the outer layer : spherulitic structure in *Kaneharaia* and composite prismatic structure in *Phacosoma*. However, these authors did not examine the shell microstructure of dosiniine species from the Cenozoic of the North Pacific, including *K. ausiensis*.

Thus, the lack of enough information on hinge structure and shell microstructure prevents us from understanding the detailed relationship among the *Kaneharaia* and other dosiniines from the Cenozoic of the North Pacific.

Recently, it has become clear that some molluscan genera originated in the northeastern Pacific and then migrated to the northwestern Pacific during the early middle Miocene (Vermeij, 1991 ; Amano *et al*., 1993 ; Matsubara, 1994 ; Reid, 1996 ; Amano and Vermeij, 1998 ; Amano, 1998). If we can make clear the close phylogenetic relationship between *Kaneharaia* and the American *Dosinia* species, it should be possible to judge whether *Kaneharaia* is another example of a westward spreading genus or not.

Fortunately, we were able to collect some well preserved specimens of *Kaneharaia ausiensis* (Ilyina) from the Miocene of Sakhalin and also examined previously undocumented specimens of *K. ausiensis* from the Pliocene of Hokkaido and of *K.* sp. from the Miocene of Kodiak Island. Here we examine the morphology of this material in detail and the shell microstructure of *K. ausiensis* and the Recent *Dosinia* species as well in order to clarify the evolutionary history of *Kaneharaia*.

Materials

A number of fossil specimens identified as *Kaneharaia ausiensis* were collected from the following four localities (Figure 1) : Loc. 1, river bank about 2 km upstream of Lesnaya River in southeastern Sakhalin ; early middle Miocene Ausinskaya Formation : Loc. 2, roadside cliff about 2.5 km north of Baykovo in southwestern Sakhalin (the type locality of *Dosinia ausiensis* Ilyina, 1954) ; early middle Miocene Ausinskaya Formation : Loc. 3, roadside cliff about 500 m northwest of Kotobuki Bridge in Kamitokushibetsu, Hokkaido ; middle Miocene Shibiutan Formation : Loc. 4, bank of the Horonitachibetsu River near Numata dai-go in Hokkaido ; early Pliocene Horokaoshirarika Formation yielding the Pliocene index fossil, *Fortipecten takahashii* (Yokoyama). These specimens are housed at Joetsu University of Education (JUE).

Five fossil specimens identified as *Kaneharaia* sp. were provided by Emeritus Professor Saburo Kanno of the University of Tsukuba. These specimens are from the middle Miocene Ejoviy Horizon of Korf Bay in eastern Kamchatka and from the early middle Miocene Narrow Cape Formation on Kodiak Island, Alaska. Detailed information on these localities are unfortunately unknown. These are also stored in Joetsu University of Education (JUE). Besides these specimens, we examined the type specimens of *Kaneharaia kannoi* and *K. kaneharai fujinensis* stored in the Museum of Natural History of Tohoku Univeristy (IGPS).

We examined the shell microstructure of two fossil and four Recent species (Table 1).

Systematic notes on northern Pacific species

Family Veneridae Rafinesque, 1815
Subfamily Dosiniinae Deshayes, 1853
Genus ***Kaneharaia*** Makiyama, 1936

Comparison.—As pointed out by Makiyama (1936), Hatai (1938) and Masuda (1967), *Kaneharaia* and *Dosinia* share many features such as absence of the escutcheon and lamellated concentric ribs, and presence of a wide triangular

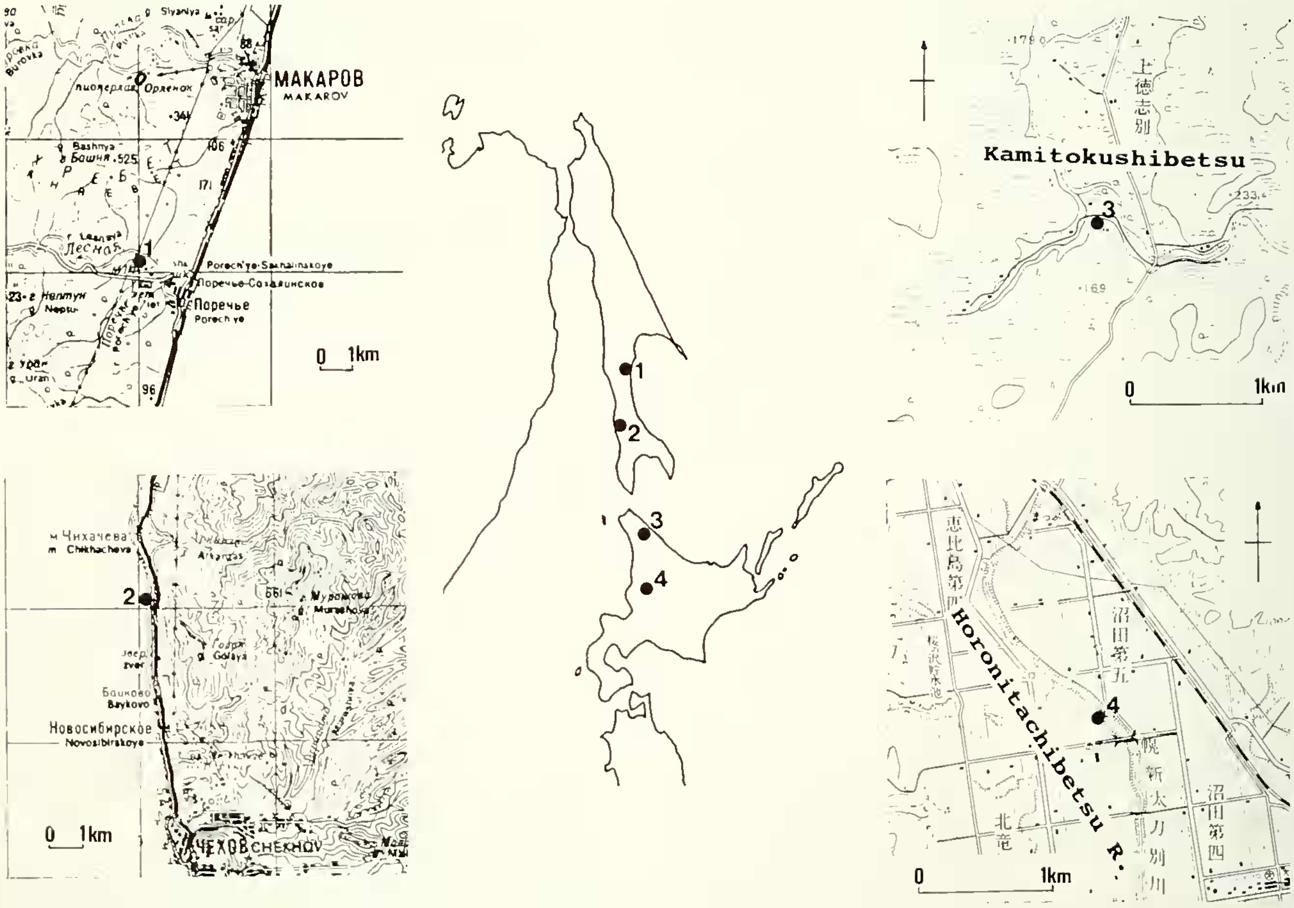


Figure 1. Collecting localities of *Kaneharaia* (using the topopgraphical maps "Occhube" and "Moseushi", scale 1 : 50,000, published by Geographical Survey of Japan).

Table 1. Shell structure of outer layer of Dosiniinae

Species	SSO**	Age	Localities and formations
**Kaneharaia ausiensis* (Ilyina)	sph+fcl	Miocene	Ausinskaya F., Sakhalin (Loc. 1)
K. kaneharai (Yokoyama)	sph+fcl	Miocene	Kubota F., Fukushima Pref.
**Dosinia discus* (Reeve)	fcl	Recent	Florida in USA
**D. dunkeri* (Philippi)	fcl	Recent	Panama
**D. ponderosa* (Gray)	fcl	Recent	California in USA
Phacosoma japonicum (Reeve)	cpr	Recent	Ohita Pref.
P. japonicum (Reeve)	cpr	Pleistocene	Omma F., Ishikawa Pref.
P. japonicum (Reeve)	cpr	Pliocene	Tatsunokuchi F., Miyagi Pref.
P. troscheli (Lishcke)	cpr	Recent	Fukuoka Pref.
P. tomikawensis (Takagi)	cpr	Pleistocene	Omma F., Ishikawa Pref.
P. tatunokutiensis (Nomura)	cpr	Pliocene	Tatsunokuchi F., Miyagi Pref.
P. hataii (Masuda)	cpr	Miocene	Kubota F., Fukushima Pref.
**P. akaisiana* (Nomura)	cpr	Miocene	Yatsuo G., Toyama Pref.
P. kawagensis (Araki)	cpr	Miocene	Mizunami G., Gifu Pref.
P. nomurai (Otuka)	cpr	Miocene	Mizunami G., Gifu Pref.
Austrodosinia anus (Philippi)	cpr	Recent	New Zealand
**Pectunculus exoleta* (Linnaeus)	cpr	Recent	Galcia in Spain

* Species treated in this study. The data of other species are based on Hikida (1996).

** Shell structure of outer layer (sph ; spherulitic structure, fcl ; finely crossed lamellar structure, cpr ; composite prismatic structure, see *also* Hikida, 1996)

pallial sinus. In addition to these characters, we found that both genera have a subumbonal pit on the hinge plate (Figures 2 1-5, 13b, 3 1, 3, 6b, 11a) and sometimes have a brown-coloured shell surface.

The above features are not observed in *Phacosoma* Jukes-Brown, 1912, *Dosinella* Dall, 1902, *Dosinorbis* Dall, 1902 and *Austrodosinia* Dall, 1902 (Figures 3-2, 4, 5, 10 ; see *also* Fischer-Piette and Delmas, 1967). *Pectunculus* Da Costa, 1778 lacks not only the escutcheon, but also the subumbonal pit (Figure 3-8).

Morphologically, *Kaneharaia* differs from *Dosinia* by having a narrower thin plate above the nymph, a thick middle cardinal tooth of both valves, and a long anterior cardinal tooth in the left valve extending to the basal line of hinge plate.

As already pointed out by Kobayashi *et al.* (1968), Shimamoto (1986) and Hikida (1996), the inner layer throughout the Dosiniinae has the same microstructure (homogeneous structure). According to Hikida (1996), the outer layer of *Kaneharaia* is spherulitic in structure while in *Phacosoma, Austrodosinia, Pectunculus* and *Dosinella* the outer layer has a composite prismatic structure (Table 1).

We have found that the outer layer of *K. ausiensis* from Sakhalin (Loc. 1) has a spherulitic structure like *K. kaneharai*, but also was a finely crossed lamellar structure near the beak and ventral margin. On the other hand, the outer layers of *Dosinia discus* and *D. ponderosa* are composed totally of the finely crossed lamellar structure (Figure 4). On *D. ponderosa*, our observation supports the results by Carter and Lutz (1990), not by Taylor *et al.* (1973). Adding *D. dunkeri* to these two species, it has become clear that all the species of *Dosinia* here examined have the same finely crossed lamellar structure (Table 1). Thus, the outer shell microstructure of *Kaneharaia* has the features partly in common with *Dosinia*, but not with other dosiniines.

From the above morphological and shell microstructure data, we conclude that *Kaneharaia* is close to *Dosinia* than any other genus within the Dosiniinae.

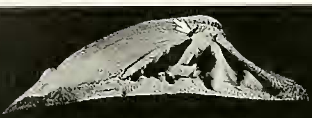
Remarks on American species.—*Dosinia* mathewsonii Gabb, 1869 was described from the upper Oligocene San Ramon Formation of California (Figure 2-7a, b). This species is characterized by the absence of the escutcheon, and presence of many wide concentric ribs, a subumbonal pit (Figure 2-9) on the hinge plate, and a brown-coloured shell surface. It is especially allied to *K. ausiensis* in having an almost identical shell shape and number of concentric ribs (15 between 10 mm and 20 mm from beak). Although no information on the pallial sinus shape of "*D.*" *mathewsonii* could be obtained, it is most probably included in the genus *Kaneharaia*.

When she examined the dosiniines from the early middle Miocene Astoria Formation in Oregon, Moore (1963) synonymized *Dosinia* mathewsonii with *Dosinia whitneyi* (Gabb, 1869). However, *D. whitneyi* is based on a single fragment. It is too difficult to obtain any information on the inner structure of *D. whitneyi*. For the above reasons, we do not use the species name *D. whitneyi*. The Astoria specimens would be better included in *Kaneharaia* rather than *Dosinia*, because the anterior cardinal tooth in the left valve extends to the basal line of the hinge plate and the plate above the nymph is narrow. However, there is also no information on pallial sinus shape in the Astoria specimens. Therefore, it is difficult to conclude whether the Astoria species can be accurately included in the genus *Kaneharaia*.

Kaneharaia ausiensis (Ilyina, 1954)

Figures 2—1-5, 8, 10-12, 14-16 ; 3—14

Dosinia ausiensis Ilyina, 1954, p. 228, 229, pl. 18, figs. 7, 8 ; Zhidkova *et al.*, 1968, p. 107, 108, pl. 5, fig. 2, pl. 18, figs. 7, 8.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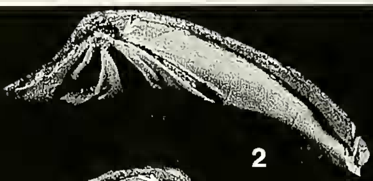
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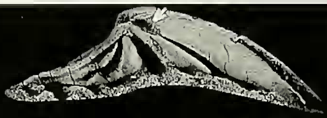
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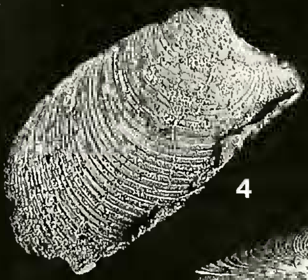
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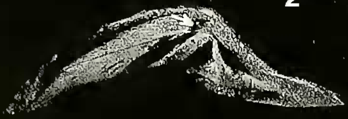
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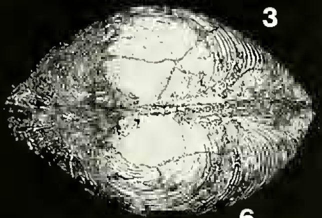
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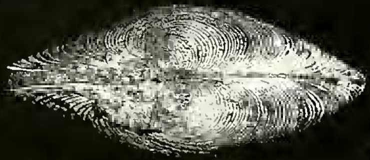
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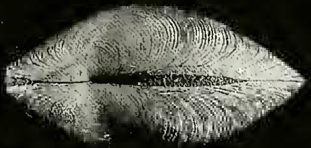
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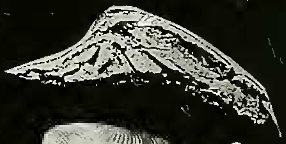
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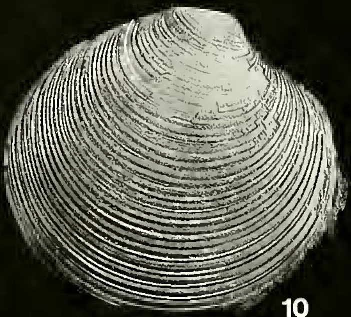
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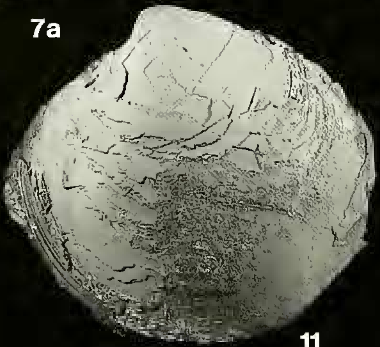
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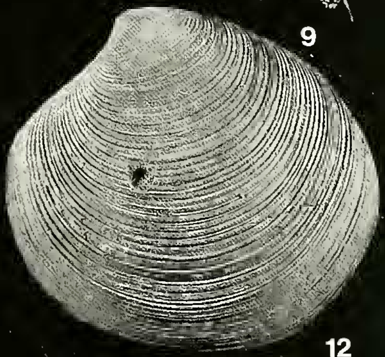
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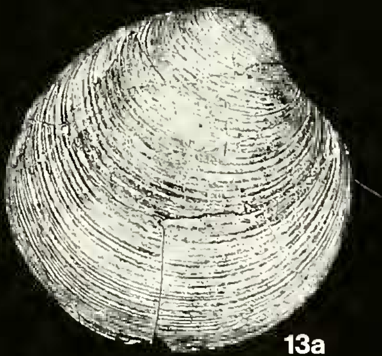
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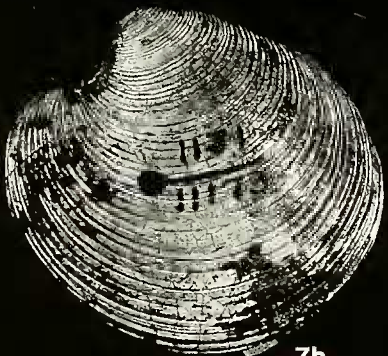
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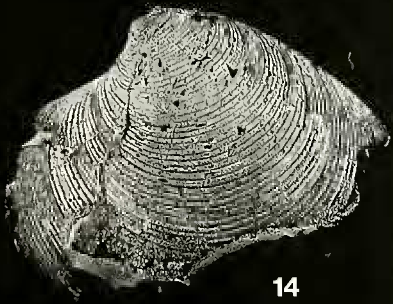
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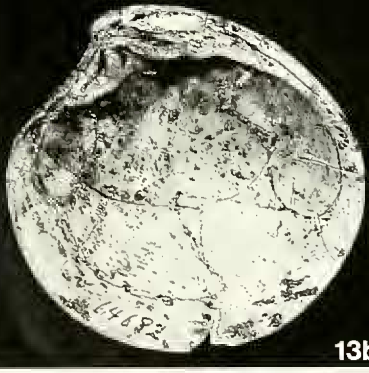
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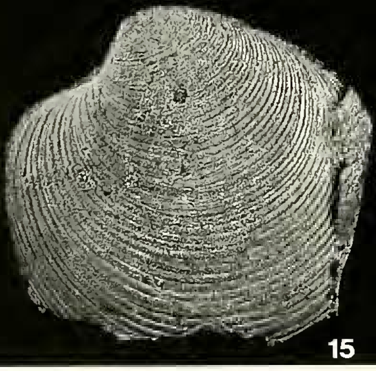
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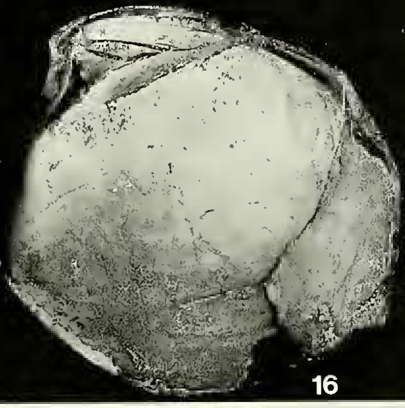
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Dosinia mirabilis Uozumi (MS). Fujie *et al*., 1964, pl. 6, fig. 4.
Dosinia (*Kaneharaia*) *kaneharai kannoi* Masuda. Masuda, 1967, pl. 2, fig. 9 ; Noda, 1992, p. 83, 84, pl. 4, fig. 1.
Dosinia (*Kaneharaia*) *kaneharai rumoiensis* Amano, 1983, p. 50, 51, pl. 4, fig. 12, pl. 5, figs. 1, 5, 10.
Dosinia (*Kaneharaia*) *kaneharai uandiensis* Sinelnikova *in* Gladenkov *et al*., 1987, p. 35, pl. 7, figs. 4, 6.
Dosinia (*Kaneharaia*) *ausiensis* Ilyina. Gladenkov *et al*., 1987, p. 35, fig. 3 ; Amano and Sato, 1995, p. 7, figs. 4-3, 6, 12 ; Amano *et al*., 1996, p. 637, figs. 4-3, 8.
Dosinia (*Kaneharaia*) *kaneharai* Yokoyama. Shimizu and Fujii, 1995, fig. 6.

Type Locality.—Klyuch Bezimyaniy (Japanese name, Ausi) in Chekhov district, southwestern Sakhalin (Loc. 2) ; early middle Miocene Ausinskaya Formation. Holotype, VNIGRI no. 7/6819.

Description of Sakhalin specimens.—Shell medium in size (47.4 mm in maxmum length), suborbicular in outline, moderately inflated. Anterodorsal margin slightly concave, passing into well rounded ventral margin ; posterodorsal margin broadly arcuate. Beak protruding, weakly prosogyrate, anteriorly situated. Surface sculptured by dense concentric ribs ; concentric ribs 15-17 in number between 10 mm and 20 mm from beak, flattened near beak but becoming rounded and elevated near ventral margin. Lunule long, narrow, shallow, and not depressed by any distinct groove. Escutcheon lacking. Hinge plate consisting of one anterior lateral tooth and three cardinal teeth ; middle cardinal tooth of right valve thick and simple ; anterior lateral tooth of left valve rather large. Subumbonal pit small, situated at uppermost part of nymph plate. Pallial sinus rather shallow and triangular in shape.

Remarks.—The Sakhalin specimens have the same shell characters as the Hokkaido specimens other than shell size : the Pliocene Horokaoshirarika specimen attains 60.6 mm in maximum length while that of the type specimen is 55 mm.

When they examined the fossil fauna from the Ausinskaya Formation in Novoselovo of southwestern Sakhalin, Amano *et al*. (1996) considered the following two subspecies to be junior synonyms of *D*.(*K*.) *ausiensis* : *D*.(*K*.) *kaneharai rumoiensis* Amano, 1983 and *D*. (*Kaneharaia*) *kaneharai uandiensis* Sinelnikova, 1987. They also considered that the specimens illustrated by Masuda (1967, pl. 2, fig. 9) and Noda (1992, pl. 4, fig. 1) as *D*.(*K*.) *kannoi* can be assigned to *D*.(*K*.) *ausiensis*.

Fujie *et al*. (1964) illustrated a specimen referred to *Dosinia mirabilis* Uozumi (MS) from the Miocene Tokushibetsu Formation in Hokkaido. Judging from its subcircular shell, fine concentric ribs and dentition with a subumbonal pit, this specimen should be referred to *K. ausiensis*.

Shimizu and Fujii (1995) illustrated a specimen of *D*.(*K*.) *kaneharai* Yokoyama from the “Otogawa fauna (type II)” of Toyama Prefecture. This specimen obviously has concentric ribs much more than the typical form of *K. kaneharai* and many elevated ribs near the ventral margin. Therefore, the Otogawa specimen should be referred to *K. ausiensis* rather than to *K. kaneharai*.

Comparison.—*Kaneharaia ausiensis* resembles *Kaneharaia kannoi* Masuda, 1963 from the lower middle Miocene Heiroku Formation of North Korea in having fine concentric ribs. However, *K. ausiensis* differs from *K. kannoi* (Figure 2-6) in its less inflated shell and more numerous concentric ribs (usually 12-13 between 10 mm and 20 mm from the beak in *K. kannoi*).

K. ausiensis differs from *K. kaneharai* Yokoyama in its orbicular rather than ovate shell and has much more numerous concentric ribs (15-17 between 10 mm and 20 mm from the beak instead of 8-12 in *K. kaneharai*)

Distribution.—Early middle Miocene Ausinskaya and Uandinskaya Formations in Sakhalin, and Chikubetsu Formation in Hokkaido ; middle Miocene Togeshita, Tachikaraushinai and Shibiutan Formations in Hokkaido ; late Miocene (?) “Otogawa Formation” ; early Pliocene Horokaoshirarika Formation in Hokkaido and Joshita Formation in Honshu.

Kaneharaia sp.

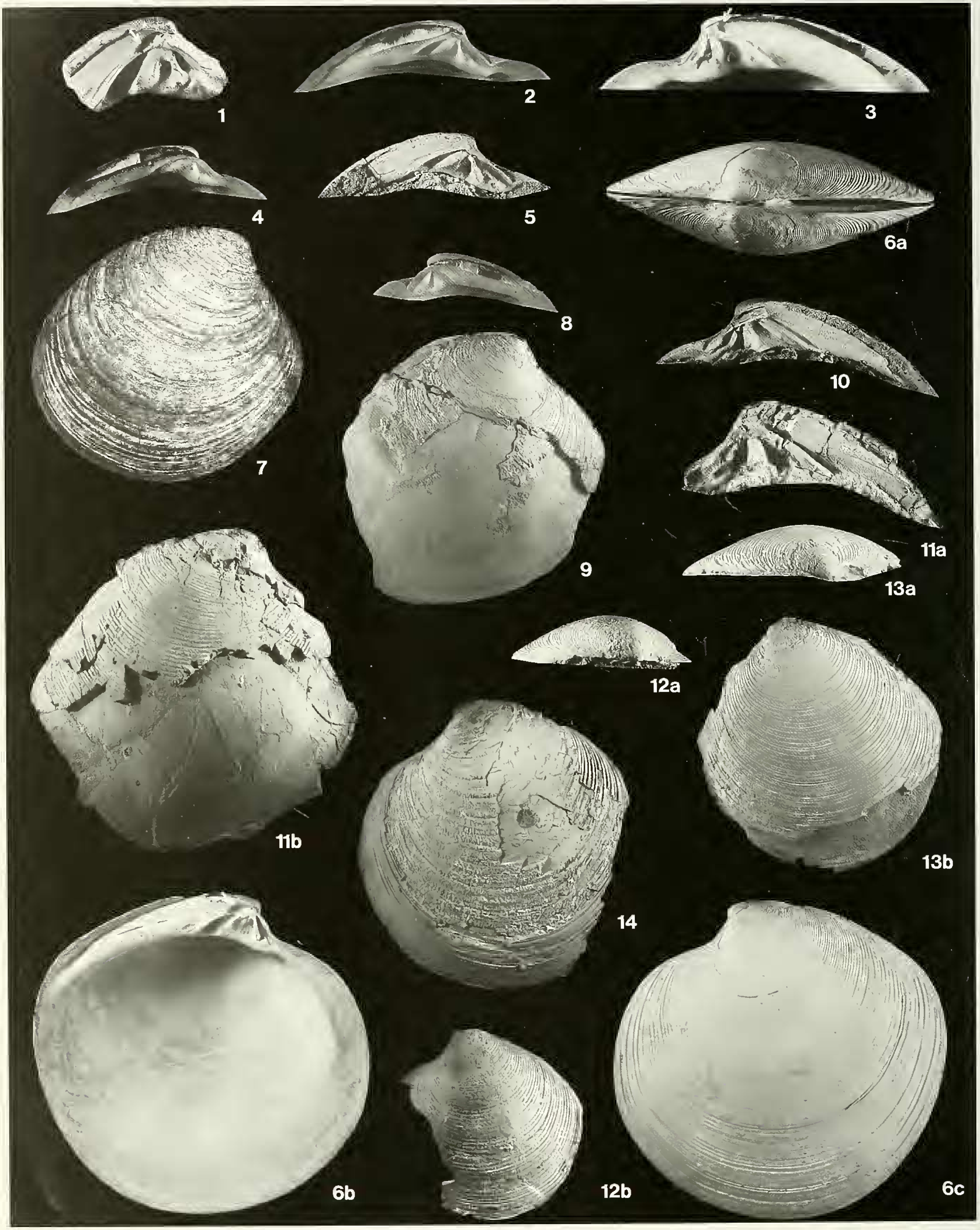
Figures 3—9, 11-13

Dosinia cfr. *mathewsoni* Gabb, Khomenko, 1933, p. 17, pl. 2, fig. 10, pl. 3, fig. 4.
Dosinia margaritana Wiedy, Slodkewitsch, 1938, pl. 88, figs. 3, 4.
? *Dosinia* (*Dosinia*) *whitneyi* Gabb, Moore, 1963, p. 73-74, pl. 24, figs. 3-10.
Dosinia (*Kaneharaia*) *rumoensis* Amano [sic], Gladenkov *et al*., 1987, p. 34-35, pl. 8, figs. 1, 2, 4, 7-11.

Remarks.—Five specimens from eastern Kamchatka, Russia and Kodiak Island, Alaska resemble *K. ausiensis* in the absence of an escutcheon and lamellated concentric ribs and the presence of a wide pallial sinus and a narrow subumbonal pit. However, these specimens have more numerous (18-22) and more flattened concentric ribs than in *K. ausiensis*, and therefore they can easily be separated from the latter at the species level.

Khomenko (1933) recorded *Dosinia* cfr. *mathewsoni* Gabb, 1869 from Korf Bay of eastern Kamchatka, with which our specimens discussed here are identical. Thereafter, Slodkewitsch (1938) reasigned Komenko's specimens to *Dosinia margaritana* Wiedey, 1928. When they described the fauna from Korf Bay, Gladenkov *et al*. (1987) identified their speci-

← **Figure 2.** **1-5, 8, 10-12, 14-16** : *Kaneharaia ausiensis* (Ilyina). 1 ; ×1.1, JUE no. 15670-1 : 3 ; ×1.2, JUE no. 15670-2 ; Loc. 1, Ausinskaya F. ; white arrow indicating a subumbonal pit. 2 ; ×1.05, JUE no. 15666-3 : 15 ; ×1.1, JUE no. 15666-2 ; Loc. 3, Shibiutan F. 4 ; ×1.2, JUE no. 15667-2 : 5 ; ×1.15, JUE no. 15667-3 : 14 ; ×1, JUE no 15667-4 : 16 ; ×1, JUE no. 15667-5 ; Loc. 4, Horokaoshirarika F. 8 ; ×1, JUE no. 15664-5 : 10 ; ×1, JUE no. 15664-1 : 12 ; ×1, JUE no. 15664-3 ; Loc. 1, Ausinskaya F. 11 ; ×1, JUE no. 15665-1, topotype, Loc. 2, Ausinskaya F. **6, 13** : *Kaneharaia kannoi* (Masuda). 6 ; ×0.9, IGPS no. 73203 : 13a-b ; ×0.8, IGPS no. 64682, holotype, Heiroku F. **7a-b, 9** : “*Dosinia*” mathewsoni Gabb. 7a-b ; ×1, UCMP no. 11173, San Ramon F. : 9 ; ×1, UCMP no. 11149, reproduced from pl. 7, fig. 5 of Clark (1918), San Ramon F. White arrows in 1, 2, 3, 5, 9, 13b shows the subumbonal pit.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6c

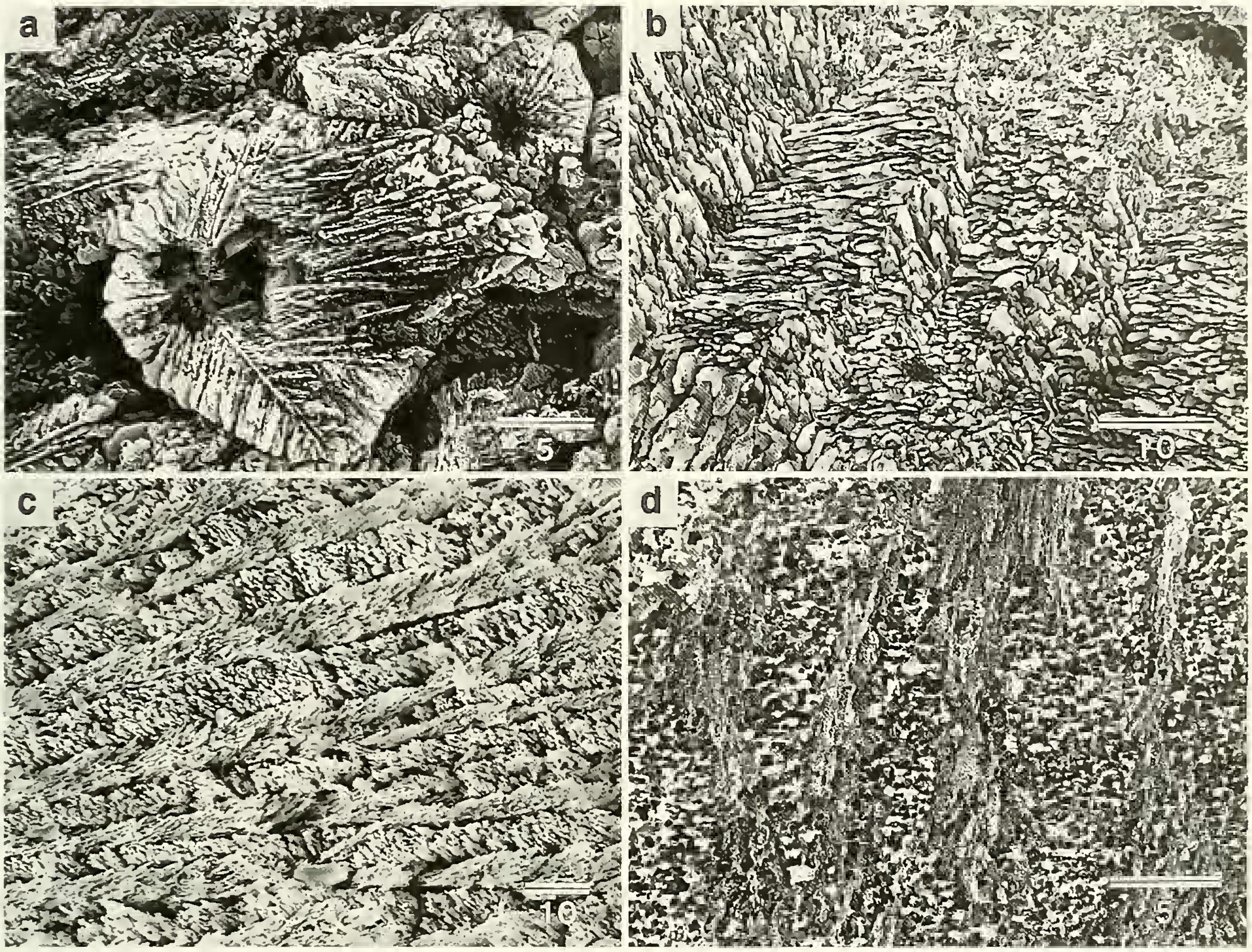

Figure 4. SEM photographs of shell microstructures of *Kaneharaia* and *Dosinia* ; scale in μm ; polished and etched (with 0.6% (v/v) HCl ; 10 sec.) section. **a** : Spherulitic structure of the outer layer of *Kaneharaia ausiensis* showing spherical to subspherical configuration of 3-12 μm in diameter. The elongated structural subunits grow radially in all directions from central parts of the spherulite. The central parts appear to be etched more quickly than the surroundings. **b** : Finely crossed lamellar structure recognized near the beak of *K. ausiensis*. Acicular crystals aggregate to form a higher structural unit (first order lamella), and they are inclined in opposite directions in the adjacent first order lamellae. Long axes of the first order lamellae are arranged perpendicularly to the outer shell surface (upper right). **c** : Finely crossed lamellar structure of the outer layer of *Dosinia ponderosa*. The first order lamellae are arranged in a feathery, radial manner toward the ventral margin (shell surface). **d** : Finely crossed lamellar structure recognized near the beak of *Dosinia discus*. Individual first order lamellae are sometimes branched, their long axes being arranged perpendicularly to the outer shell surface.

← **Figure 3. 1, 7** : *Kaneharaia kaneharai* (Yokoyama). 1 ; ×1, JUE no. 15671-2 : 7 ; ×0.8, IGPS no. 90511 ; Loc. Tanagura, Kubota F. **2** : *Phacosoma japonicum* (Reeve), ×1, JUE no. 15672, Loc. Tomikawa, Recent. **3** : *Dosinia ponderosa* (Gray), ×0.8, UC Davis, Loc. Puerto Penasco, Sonora, Mexico, Recent. **4** : *Dosinella penicillata* (Reeve), ×1, JUE no. 15673, Loc. Okayama, Recent. **5** : *Phacosoma tatunokutiensis* (Nomura), ×1, JUE no. 15674, Loc. Tatsunokuchi, Tatsunokuchi F. **6a–c** : *Dosinia discus* (Reeve), ×1, JUE no. 15675, Loc. Virginia Beach, USA, Norfork F. 8 : *Pectunculus exoleta* (Linnaeus), ×1, JUE no. 15676, Loc. Galicia, Spain, Recent. **9, 11–13** : *Kaneharaia* sp. 9 ; ×1, JUE no. 15668-2 : 13a-b, ×1, JUE no. 15668-1 ; Loc. Kodiak Is., USA, Narrow Cape F. 11a ; ×1.2 ; 11b ; ×1, JUE no. 15669-1 : 12a-b ; ×1, JUE no. 15669-2 ; Loc. Korf Bay, Russia, Ejobyi Horizon. **14** : *Kaneharaia ausiensis* (Ilyina), ×1, JUE no. 15665-2, topotype, Loc. 2, Ausinskaya F. **10** : *Phacosoma tomikawensis* (Takagi), ×1, JUE no. 15679, Loc. Kakuma, Omma Formation. White arrows in 1, 3, 6b, 11a show the subumbonal pit.

mens as *Dosinia* (*Kaneharaia*) *rumoensis* Amano [sic]. Our specimens seem to constitute a new species, but poor preservation of the Kamchakta and Kodiak specimens prevents us from establishing a new species.

Allison (1978) and Marincovich and Moriya (1990) only listed *Dosinia* and *D. whitneyi* respectively from the Narrow Cape Formation in Kodiak Island. Judging from the location, we suspect that their specimens are identical with the present species.

Distribution.—Early middle Miocene Ejoviy Horizon, Korf Bay, eastern Kamchatka, Russia; early middle Miocene Narrow Cape Formation, Kodiak Island, Alaska.

Revision of *Kaneharaia*

Dosinia (*Kaneharaia*) *kaneharai ouchiensis* was described by Kanno (1955) from the Miocene Yoshigasawa Formation in Miyagi Prefecture. Acccording to him, this subspecies can be dicriminated from *K. kaneharai* (s.s.) by its higher shell. However, the holotype and topotype specimens of *D.*(*K.*) *kaneharai ouchiensis* were slightly compressed laterally, judging from Kanno's (1955) figures and topotype specimens stored at IGPS. As mentioned by Masuda (1967), it is sometimes hard to distinguish *D.*(*K.*) *kaneharai ouchiensis* from *K. kaneharai* (s.s.). Therefore, there is no reason to follow this separation.

D.(*K.*) *kaneharai fujinensis* was established by Masuda (1967) from the Miocene Fujina Formation in Shimane Prefecture. This subspecies was separated from *K. kaneharai* (s.s.) based on an elongated shell. However, the shell outline of *K. kaneharai* (s.s.) in our specimens from the Kanomatazawa Formation shows a wide range of variation from subcircular to elongate ovate shell. The surface of the holotype of *D.* (*K.*) *kanaharaia fujinensis* is sculpted by 11 concentric ribs between 10 mm and 20 mm from the beak just the same as in *K. kaneharai* (s.s.). For the above reasons, we also do not accept the separation of *D.*(*K.*) *kanaharaia fujinensis* from *K. kaneharai kaneharai* (s.s.).

Evolutionary history of *Kaneharaia*

To sum up the discussion above, the genus Kaneharaia consists of four species in the North Pacific region,: *K. kaneharai* (Yokoyama)(middle-late Miocene), *K. kannoi* (Masuda) (early middle Miocene), *K. ausiensis* (Ilyina) (early middle Miocene-early Pliocene) and *K.* sp (early middle Miocene). Moreover, as described above, the Astoria species of "*Dosinia*" and "*D.*" *mathewsonii* most probably belong to the genus *Kaneharaia*.

There is no Oligocene record of *Kaneharaia* in the northwestern Pacific region. On the other hand, one species most probably included in *Kaneharaia* and two species of *Dosinia* have been reported from the upper Oligocene of northwest and central America. "*Dosinia*" *mathewsoni* from the upper Oligocene of California is most probably a *Kaneharaia* as discussed above. Woodring (1982) recorded *D.* aff. *delicatissima* Brown and Pilsbry, 1913 from the upper Oligocene Bohio Formation of Panama. On the Atlantic coast, Palmer (1927) illustrated *D. chipolana* Dall, 1903 from the Oligocene Silex beds of Florida.

Taking the phylogenetic relationship and fossil records into consideration, *Kaneharaia* first appeared in the northeastern Pacific during the late Oligocene.

Among the northwestern Pacific species, *K. kannoi* is confined to the early middle Miocene in northeastern Honshu and North Korea while *K. kaneharai* might be directly derived from *K. kannoi* and occurs from the middle to late Miocene in Honshu (Figure 5). *K. ausiensis* is related to *K. kannoi* and first appeared in the early middle Miocene in Sakhalin and Hokkaido. This species also occurs in the early Pliocene of Hokkaido and central Honshu. *K.* sp. is locally restricted to eastern Kamchatka and Kodiak Island in the early middle Miocene. From the early middle Miocene Astoria Formation in Oregon, *Kaneharaia*-like species have been reported.

Judging from the above distribution, *Kaneharaia* migrated to the northwestern Pacific region during the early middle Miocene time, corresponding to the Neogene Climatic Optimum. Thus, *Kaneharaia* represents another example of a mollusc that shows westward spreading in the North Pacific and is an exceptional in being an extinct genus among this group.

When she discussed the evolution of *Mercenaria* Schumacher, 1817, Harte (1998) pointed out that all Japanese "*Mercenaria*" should be placed in *Securella* Parker, 1949 because

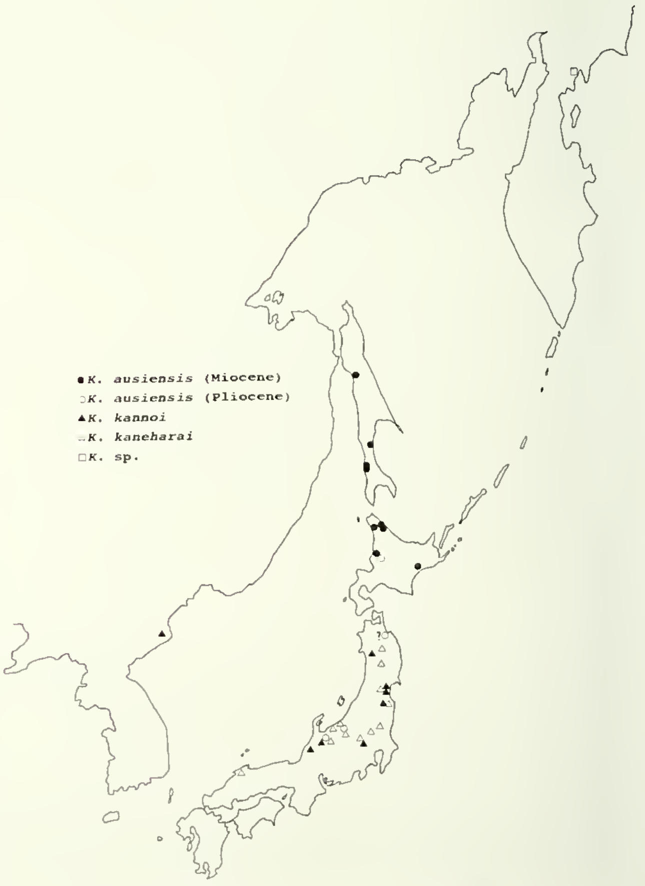

Figure 5. Distribution of *Kaneharaia*.

they lack a rugose nymph. According to her, *Mercenaria* arose from the early Oligocene *S. mississippiensis* during the late Oligocene. *Securella* first appeared in the northeastern Pacific in the late Oligocene while the oldest record of *Securella* in the northwestern Pacific date from the Miocene (Harte, 1998). Such an evolutionary pattern is very similar to that of *Kaneharaia* and *Dosinia*. It is reasonable to conclude that both genera have a common ancestor. Then, after the late Oligocene, *Kaneharaia* fluorished in the North Pacific region like *Securella*. On the other hand, *Dosinia* radiated in the Atlantic coast region like *Mercenaria*.

Besides *Kaneharaia* and *Securella*, Amano (1998) listed *Compsomyax* (Veneridae) as another example of a westward-spreading group. More examples of this type of migration will no doubt be found in other venerids.

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